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15° Factorial Values	25° Factorial Values	Differences	Ratios of Differences
− 0.83	−7.86	7.03	1.0
+12.17	+2.79	9.38	1.3
+15.72	+7.73	7.99	1.1

This is a much closer approach to unity for the ratios than in the case of facet values and the units employed may be taken as fairly close measures of the temperature factor.

A change of one facet is therefore not of equal factorial value at different points on the variation scale as far as temperature is concerned. A plotting of the data using facets as the units does not give a uniform factorial scale. Suppose temperature to be the only factor causing variation in the facet number of a particular stock but knowledge of the actual temperatures involved in the production of a particular population to be lacking and it is desired to derive the value of the temperatures from the facet values. Obviously the closer approximation is obtained by the tabulation in which each class has a facet range equal to a definite per cent. of its facet mean. Krafka's data show that even in this case the determination is not exact but certainly the error is of a much lower order than that involved in using facets as the units.

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AN EXPERIMENT ON REGULATION IN PLANTS[1]

IT is a fundamental fact that of the enormous number of buds on a tree only a few of these normally develop into branches. Every bud, however, has the capability of growth and will grow into a branch if the more apical bud or buds are removed. Even normally, in uninjured trees, some of the lateral buds grow into branches and the characteristic form and type of growth of a plant are thus determined. It is a species characteristic.

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[1] After this paper was written, my attention was called to an article by Child and Bellamy (*Science*, N. S., L, 362, 1919), in which somewhat similar experiments were reported and the same conclusion arrived at. Physiological isolation of two regions of a whole plant was produced by low temperature instead of by actual killing of tissue as in my experiments. In view of the importance of growth phenomena I believe it worth while to again call attention to the conclusions to be drawn from these facts, especially as the experiments of Child and Bellamy refer only to the influence of a growing stem on the growth of other stems and not to the influence of growing roots on the development of roots in other regions of a plant.

An analysis of the factors which retard the growth of lateral buds can best be made on plants with only a few buds, and an excellent discussion of the problem has been given by McCallum.[2] McCallum worked with the scarlet runner bean, *Phaseolus multiflorus.* The cotyledons of this bean remain at the surface of the ground and the buds in their axils never develop unless the growing stem is injured or removed. Then they invariably develop and form shoots. No amount of wounding short of removal of the growing tip will cause these buds to grow. They never grow if the terminal bud is present, no matter how much food or water is available with optimum light and temperature conditions, and they always start to grow if the terminal bud is removed and at the same time the plant is starved by cutting off cotyledons and root systems or is practically dehydrated by placing it in a very dry atmosphere.

To describe the phenomenon we say that the tip inhibits the growth of buds below it. Only a *growing* tip has this inhibitive action, for McCallum showed that if the tip is kept in a hydrogen atmosphere, which prevents its growth, the cotyledonary buds begin to grow. Later if the tip is removed from the hydrogen to air, it also will again grow.

The inhibitory influence of a growing stem tip on latent buds is exerted only downward. A growing root exerts an inhibitory influence on the development of roots above it and this influence passes upward along the stem. If the roots of a bean plant are removed, new roots will develop along the stem wherever there is most moisture. The new roots do not come from root buds as the new shoots come from shoot buds, but they arise from unformed regions of the stem. The inhibitory influence on root formation which passes upward moves along the vascular bundles and is restricted to that section of the stem immediately above in line with the point of injury to the root. This, if the stem of a bean plant is kept moist and a small notch is made (so as to cut the vascular bundle) in the stem below this moist region, the inhibitory action of the main roots will be cut off by the notch and secondary roots can now form in this moist region only on the side above the notch (see Fig. 10, p. 116 of McCallum's paper).

The inhibitory action of a growing tip in the bean on buds below is not localized in the stem perhaps we may say is not transmitted in a direct line in the stem. A notch cut half-way across the stem will not cause the cotyledonary but directly below it to grow. In *Bryophyllum,* however, Loeb's[3] experiments have indicated that the inhibitory influence of a leaf on the growth of axillary buds passes downward in the same sector of stem as the leaf itself. Moreover the inhibitory influence appears to be of the nature of material flowing, because the pathway of the inhibitory influence is affected by gravity. This is illustrated in Figs. 11, 12 and 13, pp. 349 and 351 of Loeb's paper. This influence of gravity is a fundamental fact whose importance for the explanation of regulation phenomena must not be overlooked.

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[2] McCallum, *Bot. Gaz.*, XL, 97 and 241, 1905.

It is obvious to one who seriously contemplates the facts of regulation that the influence of one part over another in the organism must be either similar to nerve influence and depend on living protoplasmic continuity between the parts, or due to the actual transport of material from one region to another. Unless we are to assume the existence of a guiding all powerful form-determining spirit or force, which is as difficult to prove as to disprove, there is no other than these two explanations. These we know to be two means of "action at a distance" in animals and we might expect them to be operating in a plant also.

Let us consider the second of these possibilities—transport of material. Two views are prevalent regarding the nature of this transport. (1) A growing stem may be supposed to form material which inhibits shoot formation and a growing root to form material which inhibits root formation.[4] These special inhibition substances pass downward and upward in the stem respectively. Polarity is a direct consequence of the formation of these substances and their direction of flow. Loeb has pointed out several instances of growing roots inhibiting the formation of roots in other regions of a plant of *Bryophyllum* and of even stopping the further growth of roots which had started to grow.

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[3] Loeb, J., *Journ. Gen. Physiol.*, I, p. 337 and 687, 1919.

[4] It has been suggested that a growing stem forms material which inhibits shoot formation but favors root formation. The root formative substances collect at the basal end of a cut stem and induce the formation of roots there. That this assumption will not hold is indicated by McCallum's experiments on root formation already mentioned. (Fig. 10, p. 116.) The stem of a whole bean plant is surrounded near its upper end by water held in a glass vessel. This gives favorable conditions for the development of roots but none grow so long as the roots of the plants are intact. If they are cut off new roots form, not at the base of the stem where the cut is and where root forming substances should collect, but in the water high up on the stem.

(2) In a whole plant, because of a certain morphological structure, the nutrient channels are such as to carry food material to growing regions. A plant grows at both ends and so long as these are intact and growing food flows toward them. If removed, food flows to other points and starts the growth of dormant short buds or root primordia. Once a stem or root has started growing Loeb's[5] experiments show very clearly that the mass of growth formed is proportional to the mass of materials available.

I believe that light is thrown on this problem by some experiments which I performed in 1910, while a student at Columbia University, and repeated at Princeton in 1912, but which have never been published. They are designed to divide a plant into two parts physiologically but not morphologically. A jet of steam was directed against the stem of a young bean plant between cotyledons and first pair of leaves in order to kill the tissue throughout the stem in this region. In some plants the leaves and growing tip above this region wilt and die but in many cases not only does no wilting occur but the tip continues to grow and *as rapidly or more rapidly* than control plants under the same conditions which are unsteamed. Nevertheless the *cotyledonary buds below the steamed region begin to grow and roots start to appear just above the steamed region.* If the air were sufficiently moist or the region surrounded by water there is no reason why these incipient roots should not grow out into a typ-

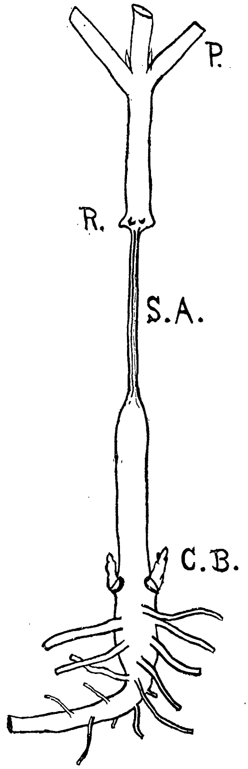

FIG. 1. Drawing showing condition of a bean plant eight days after the stem has been steamed. The top and tap root have been cut off to reduce its size for preservation. They were alive and growing during the experiment. Note that the cotyledonary buds (C. B.) grow below the steamed area (S. A.), and roots (R) appear above the steamed area. P, petioles of first pair of leaves.

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[5] Loeb, J., *Journ. Gen. Physiol.*, I, p. 81, 1918.

ical root system. I have preserved the stems of plants steamed in this way and Fig. 1 is a drawing of one of these. It will be noted that the steamed region, which was exposed for three minutes in this plant, has shrivelled to a hard woody connection about 24 mm. long. Table I gives the data regarding the growth of control and steamed plants whose tops were not killed by the steaming. The average growth for the three controls is 40.5 mm., and for the steamed plants, 59 mm. It is evident from the table also that the terminal bud has grown in the 24 hrs. immediately after steaming so that we cannot say that the steaming caused even a temporary cessation of growth of the tip.

TABLE I

RATE OF GROWTH OF STEAMED AND CONTROL BEAN PLANTS

	Plant	Time Steamed in Seconds	Length of Shrivelled Stem in Mm.	Mar. 7, Length of 1st Internode Above Leaves	Mar. 8, Length of 1st Internode Above Leaves	Mar. 11, Length of Internode		Mar. 15, Length of Internode		Total Growth in 8 Days, in Mm.
						1st	2d	1st	2d	
Controls, unsteamed. Cotyledonary buds do not grow.	1			1.5	1.5	7.5		26.0		24.5
	2			4.0	6.0	16.5	3.5	25.0	14.0	35.0
	3			5.0	10.0	34.0	2.0	50.0	17.0	62.0
March 7, 1912. Steamed. Cotyledonary buds all grow.	1	5	8.0	2.0	5.0	20.0		38.0		36.0
	2	7	5.5	5.0	7.5	9.0		21.0		15.5
	3	10	9.5	7.0	11.0	39.0		69.0	11.0	73.0
	4	15	15.0	14.0	24.0	60.0	14.0	66.0	47.0	99.0
	5	20	14.0	5.0	8.0	37.0		71.0	20.0	86.0
	6	180	24.0	13.0	18.0	47.0		48.0	10.0	45.0

It is certainly true that sap must pass up the stem of these steamed plants, otherwise the tops would remain turgid and growth occur. Root inhibiting substances, if formed, must have passed upward along with the sap. Nevertheless we find roots developing above the steamed region despite the fact that the plant has a normal living root system below. The evidence is conclusively against the existence of definite root inhibitive substances. If sap can pass upward in a steamed area we might expect that it could pass downward also. If inhibitive substances are formed by a growing stem these materials should reach the cotyledonary buds below. Nevertheless these buds develop. Since we can not necessarily argue that because material can pass up a stem it must also pass down, the evidence points against the existence of shoot inhibitive substances, but is not unequivocal.

In a plant which has been steamed the nutrient channels are the same as in a normal plant. The apical bud is growing and attracting material to it so that we cannot say this food material is now available for the cotyledonary buds as we might had the growing tip been actually cut off or prevented from actively growing by a hydrogen atmosphere. The evidence is conclusively against the view that growing points prevent the growth of dormant buds by attracting and utilizing the nutrient material.

It would seem that the inhibitive influence must be dependent on living functioning protoplasmic connections. How are we to conceive of an influence of this sort without invoking a vitalistic explanation? I believe the explanation lies in the direction developed at length with the aid of metal models by Lillie.[6] Growing points are of a different electrical potential as compared with other points and the currents so generated passing through dormant buds in the proper direction, prevent their growth. The potentials are phase boundary or membrane potentials, possibly dependent on selective ionic permeability or solubility of two phases (cell and medium) to ions, and consequently dependent or normal permeability conditions throughout the plant. Interruption of living protoplasmic connections, then, means merely the interruption in continuity of semipermeable membrances in longitudinal axes of the plant (vascular bundles?). While we may be sure that the steamed portion of a plant will conduct an electrical current, since its normal semipermeable membranes have been destroyed there is no means of obtaining a return circuit. The plant is divided into two electrical systems instead of one and behaves practically as two distinct plants. As Lillie[7] has suggested the effect of gravity on the inhibitive influence of growing stems, pointed out by Loeb, may be explained by movement of sap downward and passage of a greater current through this region because of increased electrical conductivity there. Biological polarity thus becomes electrical polarity and a given process at one region or pole is automatically accompanied by the reverse process at the opposite region or pole.

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[6] Lillie, R. S., *Biol. Bull.*, XXXIII, 135, 1917.

[7] Private communication.